THE ANATOMY AND HISTOLOGY OF THE ALIMENTARY SYSTEM OF THE HARLEQUIN CABBAGE BUG, MURGANTIA HISTRIONICA HAHN. (HEMIPTERA, PENTATOMIDAE)[1]

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The Harlequin cabbage bug, *Murgantia histrionica* Hahn, is a common and frequently very destructive pest of cruciferous plants in the southern part of the United States and south at least as far as Central America. Although it occurs, occasionally, as far north as the Canadian shores of Lake Erie, it is apparently unable to withstand ordinary winters in latitudes much farther north than the fortieth parallel (22)[3] but is thought to migrate north from its overwintering habitats each season.

METHODS

Specimens used in studies of the gross anatomy of the alimentary system were dissected *in vitro* under 1-normal saline solution and inasmuch as material was abundant specimens so used were discarded.

Tissues to be used for histological preparations were taken both from fresh material and from preserved specimens. Both methods proved satisfactory. The preservative or fixative, in all cases, was Kahle's solution (14). All histological preparations were made by the paraffin method and cut on a rotary microtome. The various structures were sectioned individually and in addition several series of sections were cut, in different planes, from the viscera *in toto* and still others from entire individuals, taken and preserved in the teneral condition. The method described by Awati (1) for softening hardened, chitinized structures was not discovered by the writer in time for use in this study.

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[3]Numbers in parentheses refer to the bibliography, page 324.

Haemalum was used as a nuclear stain and Fast Green, F. C. F. for cell walls and cytoplasm. Cell walls were not uniformly well stained and it is recommended that other stain combinations be added or that, if possible, a triple staining technique be used to obviate this deficiency.

Drawings, with the exception of Figures 1 and 2, were made with the aid of a projection microscope, the finer details being filled in, freehand, during observation of the tissues under high power or oil immersion objectives.

GROSS ANATOMY OF THE ALIMENTARY CANAL

At least nine distinct regions are recognizable in the alimentary canal. Three are stomodeal, three ventricular and three proctodeal. It will be noted that in this, as in many phytophagous species of Hemiptera, the ventriculus comprises by far the largest part of the alimentary canal.

THE STOMODAEUM

The *functional mouth* is a short, curved, chitinous tube, lying in the extreme anterior portion of the head capsule and opening, at its posterior end, into the *cibarium* or sucking pump. The cibarium extends nearly to the posterior margin of the head capsule, giving way, posteriad of the brain, to the *oesophagus* which extends just into the thorax (Fig. 2, Oes). In cross-section the cibarium (Fig. 3) appears V-shaped, is firmly embedded in the hypopharynx and the various parts of the tentorium and is connected to the dorsal wall of the head by its dilator muscles.

Both the functional mouth and the cibarium are preoral structures. Various authors have referred to the cibarium as the pharynx but Weber (29) and Snodgrass (28) point out that the true pharynx lies posterior to the sucking pump. In the present species the pharynx is almost obliterated and the extreme modification of the parts makes it impossible to limit, precisely, the various preoral and stomodeal structures.

THE VENTRICULUS

The first stomach or *anterior portion of the ventriculus* (Fig. 2, 1 Vent) is thin walled and of comparatively large diameter. It bears a prominent, dorsal, median raphe, several irregular lateral folds, but no ventral raphe. During the dissection of the insect *in vitro*, peristaltic waves were frequently observed in this region. The second stomach or *mesial portion of the ventriculus* (Fig. 2, 2 Vent) is a smooth walled tube, dilated, in active specimens, near its posterior end, to form what may be a storage space somewhat analagous to the crop of other insects. In hibernating specimens this dilatation was much less pronounced and in contrast to that of active specimens contained little or no food residue. Histological examination indicates that it should not be considered a separate division of the ventriculus. The third stomach or

posterior portion of the ventriculus (Fig. 2, 3 Vent) is remarkable in that it bears four rows of rather disc-like caeca. These will be more fully discussed in connection with their histology.

THE PROCTODAEUM

The proctodaeum, like the stomodaeum, is very short. It consists of a small caliber *anterior intestine* (Fig. 1, Ant Int), a large, thin walled *posterior intestine* (Fig. 2, Rect Sac) or rectal sac and a narrow *anal canal*, (Fig. 14) the latter contained within the anal capsule. During dissection the posterior intestine was occasionally observed to contract suddenly, as if expelling its clear, liquid contents, following which action it slowly regained its former, distended appearance.

Arising from the ventral wall of the anterior intestine is a pouch (Fig. 1, Fig. 2, Ileum?) into which the four Malpighian tubules empty. Breakey (7) reports two such diverticula in *Anasa tristis*, with two Malpighian tubules emptying into each one and various similar structures are found in other Hemiptera. Bearing in mind that in most insects the Malpighian tubules empty directly into the variously modified ileum and that in the present species the proctodeaum is so greatly reduced, one is moved to ask whether the diverticulum may not, itself, be an extremely modified ileum.

The Malpighian tubules lie in an apparently but not really tangled mass, dorsal to the posterior portion of the ventriculus, and end blindly. They are shown in the drawings as being cut off near their origins. It is interesting, in view of their mode of origin by evagination from the intestine, that although they are looped upon themselves and each other in almost every conceivable manner they were never found to be knotted or tangled. Their length is considerable, one which was measured by the writer being over twenty-five millimeters long. They are held together in a mass by connective tissue, but in no case were they found to be inserted into the wall of the alimentary canal nor bound by the peritoneal sheath of the alimentary tube.

THE HISTOLOGICAL STRUCTURE OF THE ALIMENTARY CANAL

THE STOMODAEUM

The *cibarium* (Fig. 3) is entirely chitinous and is, according to Snodgrass (28), "truly a preoral structure. . . . Its concave floor is formed by the adoral surface of the base of the hypopharynx, flanked by the suspensorial sclerites of the latter; its roof, or anterior wall, is the epipharyngeal surface of the clypeus." It consists, in the present species, of a thick walled groove which forms the ventral half of a tube, the dorsal half of which is the thin, elastic operculum. Arising from the dorsal mid-line of the operculum is a row of chitinous tendons on which are inserted the dilator muscle fibers. These muscles originate on the clypeus, lateral to the mid-line, so that in cross section of the head capsule they form a V. No other muscles are present in the cibarium. When the dilator muscles of the cibarium are relaxed the operculum is folded into the groove. When these muscles contract, it is raised, forming a canal, rhomboidal in cross section and with greatly

increased capacity. It is by means of the suction thus produced that the insect ingests its liquid food. The return of the operculum to its normal position is effected by its natural elasticity.

Ventrad of the brain the cibarium merges into the greatly reduced *pharynx* which, in turn, opens into the *oesophagus*. Its walls are continuous with the chitinous intima of the oesophagus. This is surrounded by a columnar epithelium by which, apparently, it is secreted. In the same region a well developed band of circular muscles appears, forming a sphincter which, undoubtedly, aids in preventing the anterior movement of food from the ventriculus during the suctorial process. Also, according to Bugnion (4), it pushes the liquid food along its way. Further posteriad a few scattered longitudinal muscle fibers are found entad of the circular layer. The oesophagus, ventriculus and intestine are enveloped in a thin peritoneal sheath which is frequently difficult to demonstrate. There is, however, no question as to its presence.

The oesophageal intima appears to nearly fill the canal formed by the epithelial layer of cells (*vide*, Fig. 4 and Fig. 5). It is projected a short distance into the lumen of the ventriculus (Fig. 5) and may have, in a passive way, some valvular action. The writer was unable to determine whether the intima is composed of a solid mass of very transparent chitin, of intersecting membranes or of chitinous strands. Perhaps some microchemical tests, such as described by Campbell (8) would be of assistance in answering this question.

Just anterior to the stomodeal valve the order of muscle layers of the oesophagus is reversed, the longitudinal muscles coming to lie outside the circular layer. Obviously, however, this reversal does not mark the point of junction of the stomodaeum and the ventriculus, because in none of the specimens studied histologically was there any change in the nature of the epithelium at this point. Besides, the junction is clearly shown at a point further posteriad.

The oesophagus widens slightly at its posterior end and the cells of the epithelium become elongate, extending, slightly, into the lumen of the ventriculus. This may be clearly seen in Figure 5. The juncture of the stomodaeum and ventriculus is marked by the abrupt change in the cells of the epithelial layer from the elongate type just mentioned to the shorter, more regular, but still columnar type characteristic of the entire mesenteron. Both longitudinal and circular muscles are demonstrable in this region but the latter, in particular, are scarce. Hence any valvular function must be accomplished by the pressure of food material in the ventriculus on the projecting tube of oesophageal intima. If this is not sufficient to prevent regurgitation, the action of the sphincter, previously mentioned, provides an adequate supplement.

THE VENTRICULUS

The ventriculus as a whole conforms to the typical histological pattern. It is lined by a layer of epithelial cells, usually columnar in form and resting on a thin basement membrane which is surrounded, in turn, by circular muscles, longitudinal muscles and a peritoneal sheath. Nowhere is there evidence of a peritrophic membrane. Throughout

the ventriculus the free margin of the epithelial cells bears a striated border except during the active secretory phase. Secreting cells were observed only anterior to the dilated portion of the second stomach. Secretion is of the apocrine type, the fluid to be secreted accumulating in the distal end of the cell which becomes distended and is finally pinched off, leaving the rest of the cell intact. The secretion is subsequently released into the lumen of the ventriculus and the cell, after a period of rest, may again become active. Snodgrass (28) describes this as the typical method of secretion in adult insects. As might be expected, no nidi of regenerative cells were observed.

Yung-Tai (31) and others maintain that secretions are in the form of diffusible liquids and that such processes as described above are the discharge of cytoplasmic disintegration products. The present investigations are not of such nature as to throw any light on this question.

The writer has not seen the term *apocrine* used in entomological literature but it is in common use by histologists in the medical profession (21).

The *first stomach* (Vent 1) is thin walled and the musculature is much reduced. It should be noted that the large diameter of this region is not caused by distension. The epithelial cells appear, rather, to be crowded. It is also interesting to observe that in spite of the fact that both longitudinal and circular muscles are comparatively fewer in this region than in any other part of the alimentary canal, this is the only place where peristalsis was seen to occur during dissection.

Malouf (18) states that in *Nezara viridula*, another pentatomid, this region is lined by a chitinous intima and he, therefore, considers it to be a part of the stomodaeum. No trace of a chitinous intima is present in this part of the alimentary canal of *Murgantia* and there can be no question but that in this species it is definitely a part of the ventriculus.

The *second stomach* (Vent 2) is not remarkable anterior to its dilated portion, it being the least specialized part of the entire alimentary canal. It will be observed (Fig. 9) that the epithelial tissue in the enlarged region has been stretched until the cells have assumed a cuboidal in place of a columnar form. Further evidence of distension is the fact that if the bulb is punctured during dissection the contents are forcibly ejected. The dilatation is never obliterated in such cases nor during hibernation, but this may indicate either that the muscles have lost their tonus or that some progress has been made in the evolution of a permanent structure. No sections were made from hibernating specimens so the histological structure of the bulb in its reduced condition is unknown. Posteriorly the columnar form of epithelial cells is resumed.

Nearly to the posterior end of the second stomach there is a slight elongation of the cells of the epithelium, accompanied by a slight concentration of circular muscle fibers (Fig. 10). This suggests the possibility of a valvular action controlling the passage of food or food residues into the third stomach. The presence of such a valve would aid in explaining the pressure apparent in the bulbous region just anterior. The need, if any, for the retention of food or food residues in the second stomach or for the regulation of their passage into the

third stomach must remain unexplained in a purely morphological study. However, the question is interesting and its solution might throw additional light on the function of the gastric caeca of this and related insects.

The *third stomach* (Vent 3) is distinguished by the four rows of caeca which are formed by evagination (12) from the embryonic ventriculus. Each caecum is disc shaped and consists, apparently, of an extremely thin wall of epithelial cells, which are stretched beyond recognition. The nuclei of the epithelium are shown (Nuc Epl) in muscles are found in the caecal walls. Glasgow (12) reports that the Figure 11. No muscles are found in the caecal walls. Glasgow (12) reports that the caeca are filled with specific bacteria which are transmitted from generation to generation through the embryo. These bacteria are said to prevent the infestation of this region of the ventriculus by other forms. This is considered to be beneficial to the insect and Weber (29) terms the caeca, descriptively, *symbionten krypten.* The sectioned material does not show recognizable bacterial forms, but this is undoubtedly a result of the action of the reagents used in the histological preparation of the tissues.

The alimentary canal proper, in this region, is of small caliber. When it is contracted the epithelial cells are columnar but when it is distended they assume a cuboidal form. Both circular and longitudinal muscles are present and lie close to the epithelium. The wall is, therefore, quite compact. The peritoneal membrane is folded around and between the rows but not between the individual caeca and lies very close to the enclosed structures.

THE PYLORUS AND THE PROCTODAEUM

Immediately posterior to the caecal region is found the pylorus, which marks the junction of the ventriculus with the proctodaeum.

The *pyloric valve* (Fig. 12), like the stomodeal valve, is poorly supplied with muscles. It consists of elongated cells of the ventricular epithelium, extending into the lumen of the anterior intestine, the walls of which are folded at this point. The valvular action must be largely dependent on the pressure of the contents of the proctodaeum on the extended walls of the ventricular epithelium. As in the case of the stomodeal valve the function must be the prevention of regurgitation.

The *anterior intestine* is thick walled, the thickness being due, largely, to the extreme length of the columnar epithelial cells. Longitudinal muscles are scarce and circular muscles are almost entirely lacking. There appears to be a layer of connective tissue immediately outside the epithelial layer of cells.

The *diverticulum* into which the Malpighian tubules empty is similar to the anterior intestine in histological structure and the various tissues are continuous. The epithelial cells of the diverticulum, however, are larger and are of the cuboidal type. Figure 12 shows the histological structures of the anterior intestine, the pouch and a Malpighian tubule.

In structure, the *Malpighian tubules* are very simple, appearing in cross section to consist of three or four large cells with large nuclei. The lumen of the tube is lined by a striated border. No muscle layers are present nor could a peritoneal membrane be distinguished.

Two types of cells are found in the epithelium of the posterior intestine or *rectal sac*. The more common type are large and variously shaped and in general have comparatively large nuclei. The others are narrow and crowded, occurring in groups which are irregularly distributed. Figure 15 shows the structure of both types clearly. The writer found no basis on which an attempt to homologise the groups of smaller cells with the rectal pads of other insects might be justified and no indication of their function was apparent.

No longitudinal muscles were to be found in the wall of the rectal sac but there are numerous circular muscles. It has already been noted that these muscles contract, periodically, emptying the sac of its contents. A layer of connective tissue lies between the circular muscle band and the thin peritoneal membrane.

The beginning of the *anal canal* (Fig. 14) is marked by a well-developed group of circular muscles located at the anterior border of the anal capsule and forming an anal sphincter (Fig. 14, M An Sph). It should also be mentioned that no chitinous intima could be discerned lining the proctodaeum anterior to this point. Posteriorly the canal consists simply of an invagination of the body wall as shown. The epithelium or hypodermis of the canal is continuous with the epithelium of the rectal sac.

THE SALIVARY SYSTEM

In *M. histrionica*, as in many other Hemiptera, the salivary system is both prominent anatomically and important in the nutritive processes of the insect. It, therefore, merits especial discussion.

The two salivary glands are unequally bilobed and lie dorsal to the ventriculus in the thorax, the larger and posterior lobes extending into the abdomen. Each principal gland is provided with a filiform accessory gland lying laterad and emptying by means of a long duct which extends into the head capsule, retroverts into the abdomen, is anteverted, undergoes a series of convolutions and finally opens at the juncture of the two lobes of the principal gland. From this point the salivary duct arises and passes directly into the head to unite with its bilateral opposite and empty, finally, into the chamber of the salivary syringe.

The *syringe*, a remarkable force pump, lies in a horizontal position between the arms of the tentorium, just ventrad of the cibarium. Its powerful retractor muscles are inserted on the flattened chitinous rod which is continuous with the piston and probably have their origins on the lateral arms of the tentorium and the ventral wall of the head capsule.

The following discussion is translated from Bugnion and Popoff (5): "In the Hydrocores, the accessory salivary gland serves the purpose of a reservoir, and lies beside the oesophagus, inside the thorax. The secretion of the accessory gland may, depending on the circumstances, enter the principal gland, which then serves as a reservoir, and mix with the secretion of the latter before flowing outside.

"A study of inferior forms (Aphids) shows that the salivary glands of Hemiptera are primitively tri-lobed, two of which remain contiguous while the third is more detached and is elongated.

". . . The ducts, in the Geocores, are also glandular, being secretory as well as conducting organs.

"The salivary glands of the Hemiptera are morphologically labial glands, corresponding to those of the Diptera, Hymenoptera and Orthoptera. They are also homologous with the silk glands of the silkworm, the principal glands corresponding to the gland of Filippi and the accessory gland of the silk gland proper. They arise as diverticula of the stomodaeum, thus being ectodermal in nature. . . .

"The saliva of phytophagous Hemiptera is alkaline in nature and probably has two functions, first, to cause the sap to flow and second, to dissolve the cellulose walls of the host plant cells and perhaps begin the digestion of the starch grains. The efferent salivary duct leads to the excretory canal, not to the pharynx. The digestive action of the saliva, begun outside, is probably continued in the stomach, considerable saliva being drawn up with the sap. In predaceous groups the secretion is toxic."

The walls of the principal glands consist of a single layer of cuboidal epithelial cells. No chitin was observed in the gland proper although the ducts of both the principal and accessory glands are provided with a heavy chitinous lining.

The duct of the accessory gland is inserted, the salivary duct originates and an opening between the two lobes of the principal glands occurs in an isthmus of columnar cells as shown in Figure 16a.

Unfortunately, during the making of histological preparations for the present study, none were made of the accessory salivary gland alone. However, in cross sections of a teneral individual, certain tubes appear which conform almost perfectly to Breakey's (7) description of the accessory gland in *Anasa tristis*. The cells are large, have large, deeply staining nuclei and have the general characteristics of glandular cells. Although none were observed in the actual process of secretion, many appeared to be distended.

The epithelium of the principal gland in no case appeared to be of a secretory nature. The gland is, however, usually filled with a homogeneous material which stains very evenly with Fast Green, F. C. F. In view of all the foregoing evidence the opinion is hazarded that in *M. histrionica* the salivary fluid is secreted chiefly by the accessory gland and that the function of the principal gland is largely that of a reservoir.

The salivary syringe (Fig. 17) is of the usual type. It consists of a heavy chitinous cupula, firmly attached to the tentorium, and a chitinous piston, the two being united by an elastic chitinous diaphragm. The contraction of the retractor muscles of the piston enlarges the cavity of the cupula and permits the saliva to flow in through the afferent duct. When the muscles relax, the piston is returned to its former position by the elasticity of the diaphragm, thus forcing the saliva out through the efferent duct. The entrance of the common salivary duct to the cavity of the cupula is provided with a chitinous flap which acts as a valve and prevents the salivary fluid from being forced backward through the afferent duct during ejaculation. No valve is present in the efferent duct but the walls are apparently elastic and are in apposition except when saliva is being ejected from the syringe.

Neither the efferent salivary duct nor the food canal were traced to their extremities in the beak but Weber (29) and Awati (1) state that in most if not all Hemiptera they remain distinct. The latter paper gives an excellent discussion of the structure and function of the salivary apparatus and the mechanism of suction in *Lygus pabulinus*.

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EXPLANATION OF PLATES

PLATE I

Fig. 1. Dorsal aspect of the alimentary system, including the salivary system, *in situ*. Only the proximal portions of the Malpighian tubules are shown.
Fig. 2. Gross anatomy of the alimentary canal. Only the proximal portions of the Malpighian tubules are shown.

PLATE II

Fig. 3. Cross-section of the cibarium and its supporting structure.
Fig. 4. Cross-section of the oesophagus.
Fig. 5. Longitudinal section of the oesophageal valve.
Fig. 6. Cross-section of the first stomach.
Fig. 6a. Portion of cross-section of the first stomach, highly magnified.

PLATE III

Fig. 7. Longitudinal section of the junction of the first and second stomachs.
Fig. 8. Cross-section of the anterior portion of the second stomach.
Fig. 9. Highly magnified portion of cross-section of the wall of the bulbous portion of the second stomach.
Fig. 10. Longitudinal section of posterior portion of the second stomach, showing the valvular structure occurring just anterior to the caecal region of the ventriculus.

PLATE IV

Fig. 11. Cross-section of the third stomach, including the gastric caeca.
Fig. 12. Longitudinal section through the pyloric valve.
Fig. 13. Cross-section of the anterior intestine and ileum.
Fig. 14. Longitudinal section through the anal capsule. The external wall on the right hand side of the drawing is in an abnormal position.

PLATE V

Fig. 15. Cross-section through a portion of the wall of the rectal sac.
Fig. 16. Longitudinal section through the principal salivary gland.
Fig. 16a. Longitudinal section through isthmus of principal salivary gland, taken near region of figure 16. Semi-diagrammatic.
Fig. 17. Longitudinal section through the salivary syringe.
Fig. 18. Cross-section through the salivary duct. Note the tongued and grooved nature of the cell walls.

KEY TO THE ABBREVIATIONS USED WITH THE FIGURES

Ac Gl—Accessory salivary gland.
Af D—Afferent duct of the salivary syringe.
Ant Int—Anterior intestine.
Atyp Cell—Atypical or unusual type of cell in rectal epithelium.
Bact?—Bacterial remains (?) in gastric caecum.
Chit Epi—Chitogenous epithelium.
C M—Circular muscle.
Con T—Connective tissue.
Cup—Cupula of the salivary syringe.
D Ac Gl—Duct of the accessory salivary gland.
Ef D—Efferent duct of the salivary syringe.
Epi—Epithelium.
Epi of Proct—Epithelium of the proctodaeum.
Epi of Stom—Epithelium of the stomodaeum.
Epi of Vent—Epithelium of the ventriculus.
Epi Sal Gl—Epithelium of the salivary gland.
Int—Chitinous intima.
Isthmus — Isthmus connecting the anterior and posterior lobes of the principal salivary gland.
L M—Longitudinal muscle.
Lu—Lumen.
Lu An Cnl—Lumen of the anal canal.
Lu Ant Int—Lumen of the anterior intestine.
Lu Ant Lobe—Lumen of the anterior lobe of the principal salivary gland.
Lu Ileum?—Lumen of the pouch into which the Malpighian tubules empty.
Lu Post Lobe—Lumen of the posterior lobe of the principal salivary gland.
Lu Vent 1—Lumen of the first stomach.
Lu Vent 2—Lumen of the second stomach.
Lu Vent 3—Lumen of the third stomach.
M An Sph—Muscles of the anal sphincter.
M T—Malpighian tubule.
Nuc—Nucleus.
Nuc Epi—Nucleus of epithelial cell in the wall of a gastric caecum.
Oper—Operculum of the cibarium.
Piston—Piston of the salivary syringe.
P M—Peritoneal membrane.
Rect Epi—Usual type of cell in rectal epithelium.
Rect Sac—Rectal sac or posterior intestine.
Sal D—Salivary duct.
Sal Gl—Principal salivary gland.
S B—Striated border.
Sec—Globule of secretion.
Tend—Tendon on which the dilator muscles of the cibarium are inserted.
Tend Syr—Tendon of the salivary syringe; pump handle.
Tr—Tracheole.
Valve?—Valve near the posterior end of the second stomach.
Vent Wall—Ventral wall of the cibarium.

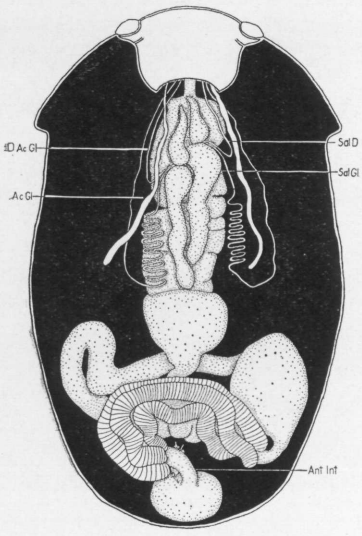
±D Ac Gl
Ac Gl
Sal D
Sal Gl
Ant Int

Fig. 1

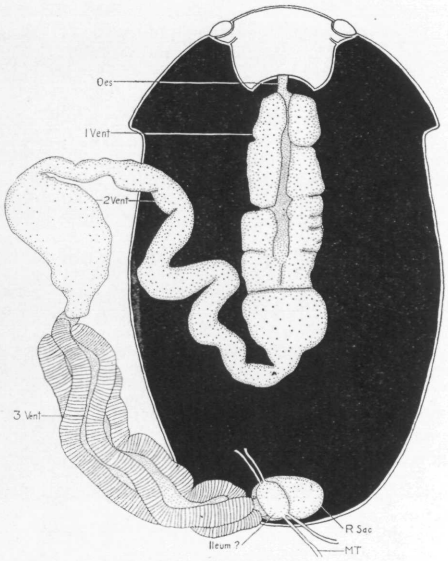
Oes
1 Vent
2 Vent
3 Vent
Ileum ?
R Sac
MT

Fig. 2

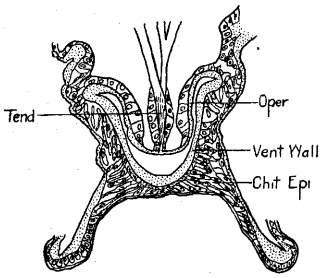

Fig. 3

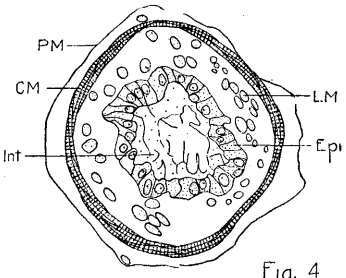

Fig. 4

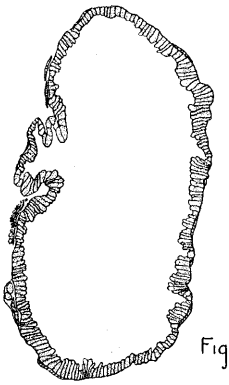

Fig. 6

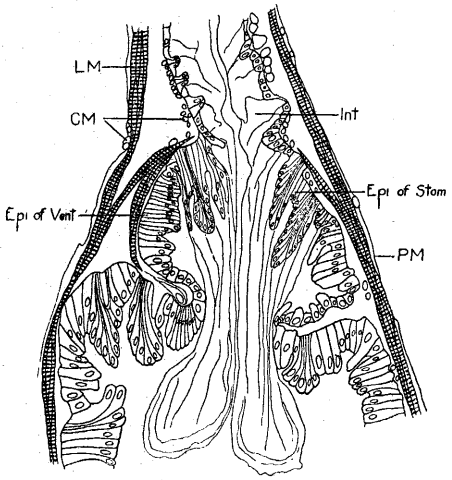

Fig. 5

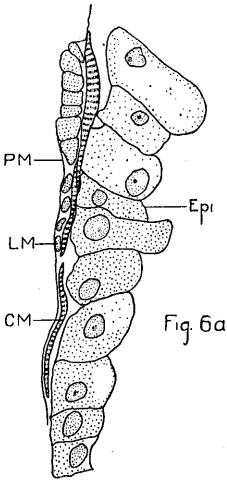

Fig. 6a

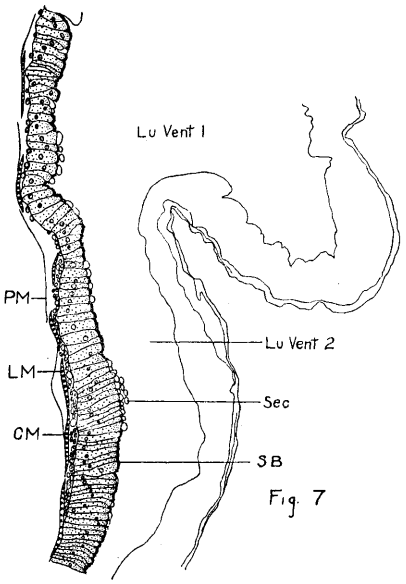

Fig. 7

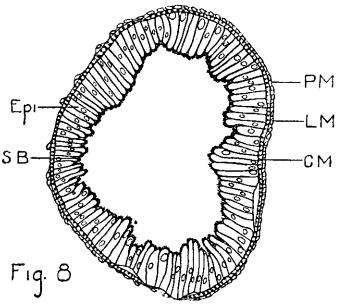

Fig. 8

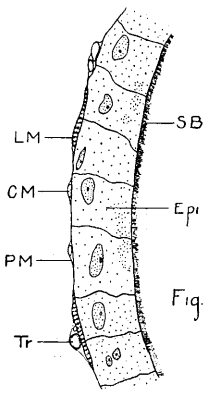

Fig. 9

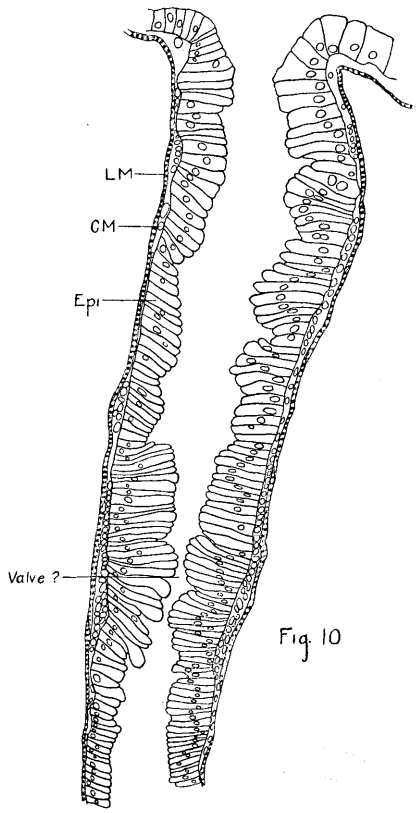

Fig. 10

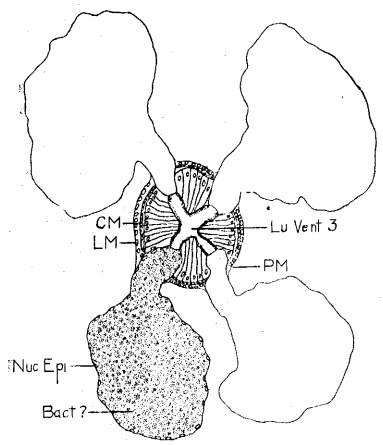

Fig. 11

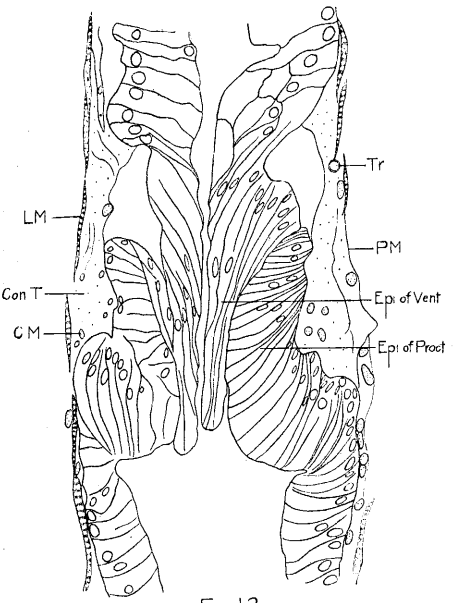

Fig. 12

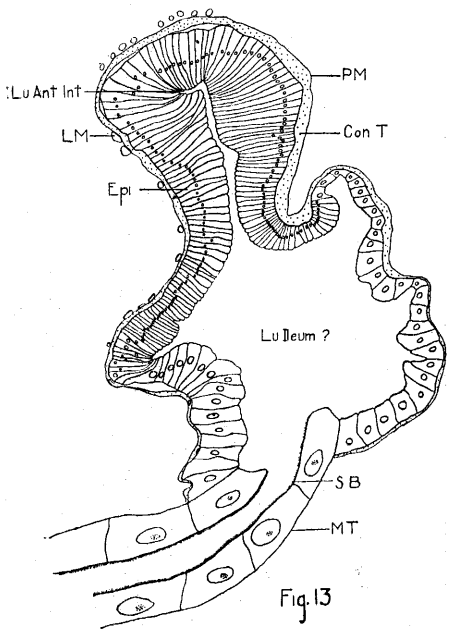

Fig. 13

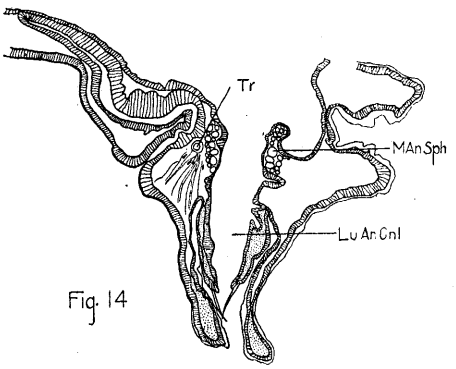

Fig. 14

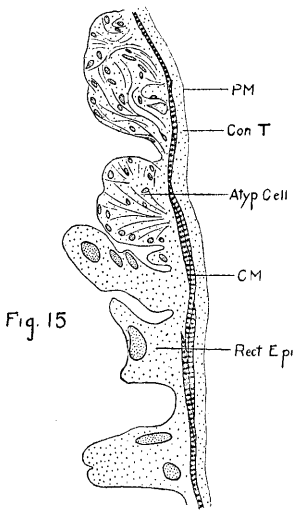

Fig. 15

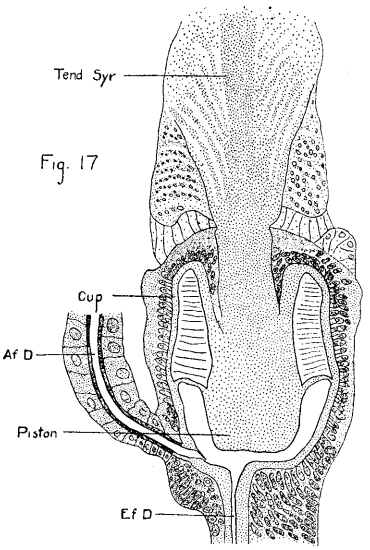

Fig. 17

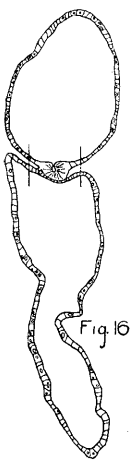

Fig. 16

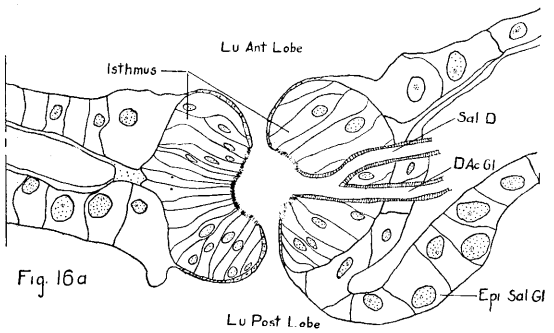

Fig. 16a

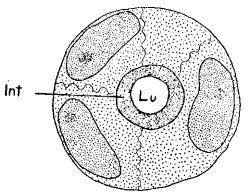

Fig. 18